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Herbicide Absorption and Transport in Honey Mesquite and Associated Woody Plants in Texas

Contents

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Introduction

According to information published in the 1960s (99), honey mesquite grows on more than half (about 22.7 million hectares) of Texas rangeland. Surveys in the mid-1980s indicated that acreages infested had changed little at about 50 percent of all rangeland in Texas (2). Several reasons are evident for this unchanged acreage including the small acreage treated each year with herbicides (< 0.5 million hectares) (103), the sometimes lack of effective treatment (32), and the rapid reinfestation of new areas (43). In addition, attitudes toward brush management have changed over the last several years and more brush is tolerated in ranch planning and retained for wildlife habitat.

Despite new attitudes and government regulations, herbicides will continue to be essential tools alone and with other management practices (mechanical, fire, biological) for weed and brush management on pastures and rangeland.

This review summarizes the work done on absorption and translocation of herbicides in honey mesquite and associated woody and herbaceous plants in Texas. Factors affecting herbicide success and environmental response are reviewed so that this reference can be used as a basis for future research and direction.

Historical Review

As early as 1948, Fisher and Young (54) reported that sodium arsenite, sodium arsenate, sodium chlorate, ammonium sulfamate, sulfamic acid, ammonium thiocyanate, 2,4-D, and 2,4,5-T were the only chemicals out of several hundred tested that were absorbed by the foliage and translocated in sufficient amounts to kill dormant buds on the underground stems of honey mesquite. However, the researchers indicated that ideal conditions of absorption and translocation of chemicals were seldom attained in the Southwest, since moist contact of the chemical with the leaf surface was required for long periods (8 hours). Increasing chemical concentration on leaf surfaces above lethal concentrations did not improve translocation.

It was reported in 1949 that an ester of 2,4,5-T applied to the foliage of mesquite was a more effective treatment than several formulations of 2,4-D or other chemicals (108). During the same year, aerial applications were made to mesquite in different seasons (55). Most effective control was obtained at the full leaf stage (spring) with ample soil moisture (90 percent canopy reduction and 25 percent mortality). By 1951, an estimated 0.2 million hectares of honey mesquite in Texas were treated commercially with broadcast foliar sprays of the ester of 2,4,5-T (61).

In 1956, Fisher et al. (57) defined the following factors responsible for the effective control of mesquite with 2,4,5-T.

1. Effective control depends upon translocation of a toxic amount of 2,4,5-T from foliage to the crown tissues.
2. Greatest translocation of 2,4,5-T occurs during a 50- to 90-day period after the first leaves emerge in the spring (most favorable time of treatment).
3. Maximum translocation of 2,4,5-T occurs when total sugar content in roots is accumulating at a rapid rate following the low level at the beginning of the full leaf stage.
4. Minimum translocation of 2,4,5-T occurs when total sugars in roots are decreasing

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rapidly and when reducing sugars are relatively abundant.

5. Most effective control of mesquite with 2,4,5-T occurs when soil moisture is adequate, a heavy foliage cover is present, and after rapid growth of new leaves and stems has ceased.
6. Effectiveness of aerial application of 2,4,5-T is reduced when either drought-restricted growth or when intermittent rainfall causes irregular foliage growth.
7. The herbicide 2,4,5-T is more effective when applied to mesquite growing on sandy loam and deep sandy soils compared with heavy clay soils, and on small plants with stems less than 8 cm in diameter compared with larger trees.
8. Carriers, whether oils alone, oil-water emulsions, or water alone, have no apparent influence on the effectiveness of 2,4,5-T applications when used at 37, 75, or 135 l ha^{-1} (liter per hectare) total volume.
9. A rate of 0.56 kg ha^{-1} (kg per hectare) of low volatile ester of 2,4,5,-T in a 1 to 3 ratio of oil-water emulsion effectively and economically controls mesquite. Increasing the amount of 2,4,5-T does not increase the percentage of mesquite killed.
10. Droplet size of sprays, formulation of 2,4,5-T, and weather factors do not appreciably affect the effectiveness of 2,4,5-T. However, these factors must be considered in ease and safe handling of the herbicide under field conditions.

Fisher et al. (53) defined the anatomy and morphology of honey mesquite and showed that the dormant buds on the underground stem of mesquite must be destroyed in order to kill the plant. Effective evaluation of absorption and translocation of the herbicide was measured by plant response in discoloration or killing of leaves, defoliation of leaves, and finally death of the plant. Hull (62) did similar studies on seedling velvet mesquite in Arizona.

Young and Fisher (107) devised a rapid method of testing the absorption and translocation of herbicides by spraying an exposed branch and observing the effect on the leaves of the sprayed branch compared with the leaves on a shielded or protected branch. Fisher and Young (56) also used a tip immersion method to test translocation by immersing the tip of a branch into a herbicide container for a period of 1 to 24 hours and observing translocation by plant effect. These methods were very useful in determining the best herbicides, formulation, chemistry, diluents, timing of application, and environmental conditions necessary for best results; although, they did not quantify herbicide absorption and translocation in plant tissue.

From these early studies, the most successful and economical broadcast herbicide treatment for honey mesquite was aerial application of a low volatile ester of 2,4,5-T (58). The herbicide was applied in a 1 to 3 diesel oil/water emulsion carrier at 37 l ha^{-1} 50 to 90 days after bud break in the spring (59). Herbicide rates tested were 0.56 to 1.1 kg ha^{-1} (60).

Although the principles as outlined were established more than 40 years ago, they are still valid today for honey mesquite control with hormone-type herbicides even though 2,4,5-T is no longer available. Fisher et al. (57) indicated that the low volatile ester and suspended acids of 2,4,5-T were more consistent in killing mesquite than either the high volatile esters or the amine formulations. Tschirley and Hull (101), Reynolds and Tschirley (91), and Valentine and Norris (102) also found that the esters of 2,4,5-T were consistently more effective on velvet mesquite.

Improved Quantification of Herbicides

The pioneering work of Crafts and co-workers (44, 45, 46, 47) improved our understanding of how assimilates move in the conducting tissue of plants and introduced us to the use of radio-labled herbicides to monitor their uptake and movement in plants. Autoradiography methods (47) indicated degree of absorption, transport, and distribution in the plant, but methods were not very quantitative. Merkle and Davis (79, 80) were first to show that picloram and 2,4,5-T could quantitatively be determined in herbaceous plant tissue (*Phaseolus vulgaris* L. var. Black Valentine bean) by use of gas chromatography (GC). Morton et al. (89) compared uptake and transport of carboxyl-labeled and unlabeled butoxyethyl ester and ammonium salt of 2,4,5-T by 3-year-old, field-grown honey mesquite by liquid scintillation counting

and gas chromatography. Absorption of 2,4,5-T was determined by assaying leaf-rinsing solutions and extracts of treated leaves. Transport of 2,4,5-T was measured by determining amounts found in stem tissue. The methods of analysis gave comparable results when extraction, cleanup, and analytical procedures were identical.

Bovey et al. (20) showed that bioassays using Puerto Rico 39 cucumber plants (*Cucumis sativus* L.) and gas chromatography to detect picloram in tropical soils gave comparable results. Sunflower (*Helianthus annuus* L.), soybeans (*Glycine max* L.), cucumber, and field bean were used as bioassays compared to GC analysis to quantify nanogram quantities of picloram in river sand and a sandy clay loam. Results from GC analysis and bioassay methods were closely correlated, but GC demonstrated less inherent variability than bioassay methods (93).

There were no differences in spray deposit on mesquite leaves whether determined fluorometrically from a fluorescent dye in the spray solution or determined chemically by gas chromatographic analysis. GC methods compared favorably in all these experiments to other means of herbicide analysis. Data in this report are for herbicides detected from plant tissue mainly by GC methods.

Foliar Absorption

Lethal amounts of foliar applied herbicides must be absorbed by leaf and stem tissue and translocated to the crown zone of honey mesquite and roots of other woody plant to effectively control growth and/or cause mortality. The following factors affect foliar absorption.

Herbicide type

Herbicides vary in rate and extent of foliar penetration. Young and Fisher (54, 56, 107, 109) found that 2,4,5-T was more readily absorbed than many other chemicals tested, including 2,4-D, by leaves of honey mesquite. This was determined by plant response to the herbicides (54, 56, 107, 109) and no actual chemical content determinations were made. Davis et al. (49) studied the uptake of picloram and 2,4,5-T in leaves of 10 woody species, including honey mesquite, and found that in most species picloram entered faster and accumulated at higher concentrations than 2,4,5-T, 14 and 48 hours after application. In other studies (48), honey mesquite leaves also absorbed picloram more rapidly and extensively than 2,4,5-T, but moisture stress reduced foliar uptake of picloram, whereas absorption of 2,4,5-T was unaffected. In winged elm (*Ulmus alata* Michx.), moisture stress did not affect absorption of picloram or 2,4,5-T. Bovey and Mayeux (28) found higher concentrations of clopyralid than 2,4,5-T, triclopyr, or picloram in honey mesquite stems and roots 3, 10, and 30 days after application to soil or foliage in the greenhouse.

More clopyralid than 2, 4, 5-T, triclopyr, or picloram was usually detected in upper and basal stem phloem and xylem in field-grown honey mesquite (31, 87). Gas chromatographic analysis of field-grown honey mesquite indicated that more than twice as much clopyralid was absorbed by leaves than picloram by 4 hours after treatment (36). After 1, 3, and 8 days, more than three times as much clopyralid was transported to the upper stem phloem as picloram.

Leaves of spiny aster (*Aster spinosus* Benth.) absorbed less 2,4-D and picloram than sunflower at 2, 4, and 6 hours after exposure (68). Picloram concentration was usually less than 2, 4-D except after 4 hours exposure in spiny aster leaves. Therefore, foliar absorption may be the limiting factor in response of spring broadcast applications of 2,4-D and picloram. Absorption of the potassium salt of 2,4-D and picloram by undisturbed stem tips compared to regrowth stem tips was greater at 2 hours after treatment but was usually no different at 4 and 6 hours (68). Main stems absorbed less herbicide at 2 and 4 hours than undisturbed stem tips but were no different at 6 hours after treatment.

When 2,4-D and picloram absorption was monitored in spiny aster from field applications, peak concentrations occurred in the leaves at 24 to 48 hours after treatment and declined up to 120 hours after treatment. Peek concentrations from broadcast applications of 2,4-D at 2.24 kg ha^{-1} and of picloram at 1.12 kg ha^{-1} resulted in about 15 to 16 $\mu g\ g^{-1}$ of herbicide per gram fresh weight of spiny aster leaves. There were usually no significant differences between herbicide concentrations in shredded and nonshredded terminal stems. No

2,4-D or picloram was detected in rhizomes of spiny aster.

In tissue culture, greatest absorption of picloram and dicamba in soybean and cottonwood (*Populus deltoides* Marsh.) occurred from agar the first 24 hours after treatment (52). However absorption remained nearly static for 14 days thereafter. More dicamba was absorbed by soybean and cottonwood tissue cultures than either picloram or 2,4,5-T.

More picloram than triclopyr was absorbed by greenhouse-grown huisache leaves by 3, 10 and 30 days following broadcast sprays applied at 1.12 kg ha^{-1} (27). The potassium salt of picloram and the triethyamine salt of triclopyr were used.

Detached leaves of Drummond's goldenweed [*Isocoma drummondii* (T. & G.) Greene.] absorbed the potassium salt of 2,4-D from aqueous solutions more slowly than did sunflower and both species absorbed less of the potassium salt of picloram than 2,4-D. There was no difference in absorption of herbicides by leaves 6 hours after exposure to solutions containing 0.5 percent (v/v) surfactant. Attached Drummond's goldenweed leaves absorbed about 50 percent available 2,4-D (diethylamine) and 25 percent of available picloram (potassium salt) within 5 days after spraying in the field during July and November.

Herbicide Formulation

Morton et al. (89) found larger amounts of 2, 4,5-T in honey mesquite leaves treated with the butoxyethyl esters of 2, 4, 5-T than those treated with the ammonium salts. Concentra-tion of 2, 4, 5-T translocated to the stems, however, was similar. Most data suggest that ester formulations of the phenoxy herbicides penetrate leaf surfaces more readily than amine salts (63). This may or may not result in greater accumulation of herbicide in the roots, since the esters are not translocated as readily as the amine salt formulations (29, 62).

Leaves of greenhouse-grown honey mesquite rapidly absorbed triclopyr from both ester and amine formulations (30). After 4 hours, about 23 percent of both formulations were absorbed from application of commercial grade triclopyr. By 24 hours after treatment, more triclopyr acid was recovered from application of the amine than the ester formulation. A large proportion of the herbicide was absorbed by the treated leaf, especially the amine formulation, but not all the triclopyr was recovered after transport because of possible degradation and lack of analysis of the ester fraction. The triethylamine salt or the ethylene glycol butyl ether esters of triclopyr were applied at 54 μg and 62 μg, respectively, to one leaf per plant per pot, on five plants, with four replications.

In another study (30), the analytical grade of the triethylamine salt and the n-butoxy ethyl ester were applied to greenhouse-grown honey mesquite leaves at 65 μg and 62 μg, respectively, with five plants per replication and three replications in a randomized complete block design. After 0, 4, and 24 hours, absorption of both forms were about equal when both the acid and ester were analyzed and added together for the ester. A majority of the ester was rapidly hydrolyzed to the acid by 4 and 24 hours after treatment.

In field-grown honey mesquite (30), more triclopyr acid (131 μg) was detected in leaves after application of the amine than the ester (39 μg) at 0 hours, but by 4 hours (105 vs. 110 μg) or 24 hours (54 vs 58 μg) no differences in triclopyr formulations were apparent. Loss of absorbed triclopyr from leaves was largely caused by transport to the stem.

Application of the monoethanolamine salt and the 2-ethylhexyl ester of clopyralid to greenhouse-grown honey mesquite leaves with a pipet indicated that about twice as much clopyralid was absorbed within 15 minutes from the ester form (26%) than from the amine form (12%) of the total recovered (37). However, after 24 hours, absorption of the ester was less than the amine. In another study (38), treated leaves of greenhouse-grown honey mesquite absorbed more clopyralid within 15 minutes (0 hours) after pipet application of the oleylamine salt compared with the monoethanolamine salt or the 1-decyl ester. After 24 hours, treated leaves absorbed and transported more clopyralid into the plant treated with the salt formulations than the 1-decyl ester.

Herbicide Mixtures

In greenhouse-grown mesquite, Davis et al. (50) found that the uptake and transport of 2, 4,5-T decreased in the presence of picloram, but the uptake and transport of picloram increased in the presence of 2,4,5-T. Increasing ratios of 2,4,5-T to picloram up to 16 to 1 con-

tinued to increase uptake and transport of picloram. The inverse effect occurred for 2,4,5-T when picloram: 2,4,5-T ratios were increased.

Paraquat reduced absorption and translocation of picloram in greenhouse-grown honey mesquite, huisache, and bean in 1 to 1 mixtures at 0.012 M each (50). In the field, paraquat increased uptake of picloram by yaupon (*Ilex vomitoria* Ait.) but did not effect transport.

Bovey et al. (36) found that addition of picloram or triclopyr to clopyralid at equal rates applied to field-grown mesquite (0.28 + 0.28 kg ha^{-1}) increased clopyralid concentrations in the leaves by 4 hours after treatment compared with clopyralid applied alone.

Baur et al. (7) studied the absorption of picloram and 2,4,5-T in detached live oak (*Quercus virginiana* Mill.) leaves immersed in aqueous solutions for up to 4 hours. Herbicide concentration ranged from 10^{-3} to 10^{-6} M; solutions were adjusted to either pH 4, 6, 7, or 8. Absorption of picloram in the presence of equimolar concentrations of 2,4,5-T exceeded that for picloram alone. Picloram had no effect on 2,4,5-T absorption.

Baur et al. (5) found that recovery of 2,4,5-T as acid and ester was greater in live oak tissues treated with mixtures of picloram (ester or salt) than in tissue treated with 2,4,5-T as the 2-ethylhexyl ester applied alone.

Carriers and Adjuvants

Fisher et al. (57) evaluated a wide range of oils and oil-water emulsions as well as water as 2,4,5-T spray carriers for control of honey mesquite. The diesel fuel oil-water emulsion (1:3) was considered equally effective and more economical to use than specially formulated oils. In some instances, use of water alone as the carrier reduced the effectiveness of the 2,4,5-T applications. Hull (62) indicated similar results on velvet mesquite. A nontoxic oil in a 1 to 4 oil-water emulsion as a carrier for 2,4,5-T resulted in considerably greater injury to the nontreated distal foliage than diesel oil as a carrier. Behrens (14) found that when diesel fuel alone was used as the carrier on greenhouse-grown plants at spray volumes of 117 and 299 l ha^{-1}, effectiveness was reduced compared with 37 l ha^{-1}. The reduced effectiveness was attributed to the phytotoxicity of the diesel fuel, which caused rapid killing of the leaves, limiting 2,4,5-T translocation. However, Bovey et al. (26) found that no differences occurred in canopy reduction of honey mesquite when water, diesel oil, or diesel oil and water carriers at ratios of 1:3, 1:9, 1:18 were used with the 2-ethylhexyl ester of 2,4,5-T in 187 l ha^{-1} diluent. Scifres et al. (94) found that absorption of 2,4,5-T ester was more rapid in a paraffin oil carrier than in diesel fuel, water, or emulsions of the oils in water carriers. No significant differences in percentage mesquite control have resulted from foam carriers (78, 97) compared with conventional sprays or addition of sufactants to the spray solution (26). Most commercial herbicide formulations have sufficient surfactant and wetting properties for wetting plant surfaces, and the addition of most sufactants or emulsifiers to the spray solution may have limited effect.

Addition of surfactant I (trimethylnonylpolyethoxyethanol) or surfactant II (4-isoprophenyl-1-methyl-cyclohexane) at 1 and 0.6 percent (v/v) of the spray solution enhanced the phytotoxicity of the triethylamine salt of triclopyr, picloram, and the butoxyethanol ester of 2,4,5-T in greenhouse-grown but not field-grown honey mesquite (34). Adjuvants, however, did enhance clopyralid activity (34, 36). Surfactant I and II at 0.5 percent by volume enhanced clopyralid absorption in field-grown honey mesquite leaves by 4 and 24 hours after application of broadcast sprays with 0.28 kg ha^{-1} of clopyralid (36). Increased uptake of clopyralid with surfactants may be partially due to enhanced spray retention caused by the surfactant (33, 34).

Organosilicone surfactants Sylgard 309 [2-(3-hydroxypropyl)-heptamethyl trisiloxane, ethoxylated, acetate EO glycol,-allyl, acetate] or Silwet L-77 (polyalkyleneoxide modified polymethylsiloxane copolymers) added to the spray solution at 0.1, 0.25, 0.2, or 0.5 percent by volume did not increase spray deposition, absorption, translocation, or phytotoxicity of clopyralid in greenhouse-grown honey mesquite (42). Mayeux and Scifres (70) found 0.5 percent (by volume) surfactant in the spray solution did not enhance absorption of 2,4-D or picloram by detached Drummond's goldenweed leaves. Mayeux and Johnson (76) indicated the addition of surfactant had little effect on absorption of picloram in Lindheimer pricklypear (*Opuntia lindheimeri* Engelm).

Meyer et al. (82) found that field-grown honey mesquite leaves were functional in herbicide uptake for about 4 days after application. However, maximum absorption apparently occurred the day of spraying. Thus, any agent or force which causes leaf removal too quickly after spraying reduces control. In most cases, it is important to use a carrier that will penetrate the waxy surface of the leaf but will not kill the leaves or cause abscission soon after spraying (95).

Spray Characteristics

Spray droplet size affects phytotoxicity depending upon species studied. In some species, herbicidal efficiency decreases as droplet size increases above 500 micrometers in diameter (63). Behrens (14) reported that droplet size, spray volume, and herbicide concentration had no direct influence, other than minor affects, on response of honey mesquite or cotton to 2,4,5-T, but that droplet spacing of 465 droplets per cm^2 was considered the maximum spacing that would maintain a high level of herbicidal effectiveness.

The addition of surfactant WK (trimethynonylpolyethoxyethanol) at 0.5 percent (by volume) of the spray solution caused increased uptake of clopyralid by the upper canopy of greenhouse grown honey mesquite (33). Enhanced uptake after 24 hours was probably a result of a twofold increase in deposit of clopyralid on the plant (33, 40). Greater deposit of clopyralid on plant surfaces after addition of surfactant was associated with reduced liquid surface tension and greater percentage of spray volume in small droplets (< 204-μm diam.). The addition of surfactant WK at 0.5 percent (by volume) of the spray solution caused a twofold increase in deposition of the monoethanolamine salt of clopyralid but not the oleylamine salt (40). There were no differences in spray deposit between spray droplet size spectrums of 160 or 330 μm Dv.5 or spray solution application of 47 or 187 l ha^{-1}.

An air-assist spray nozzle at 9.4 l ha^{-1} by volume resulted in greater initial clopyralid deposit and detection in the upper canopy of greenhouse-grown honey mesquite than application by conventional hydraulic nozzle at 9.4 or 187 l ha^{-1} (42). Air-assist application did not increase phytotoxicity compared to hydraulic nozzles. In the field, honey mesquite mortality and canopy reduction were significantly less 16 months after aerial applications of clopyralid in the 624 μm droplets treatment in two of four experiments, when compared with plots treated with smaller droplet sizes (325 and 475 μm Dv.5) (104). Mortality increased with larger spray volumes (19, 37, and 75 l ha^{-1}) particularly with 625 μm droplets. Mortality data show that larger droplets sizes require larger spray volumes for greatest efficiency.

Hand carried spray equipment with 800067, 8001, and 8015 Spraying Systems flat fan nozzles were used to obtain 37, 187 and 935 l ha^{-1} in a diesel oil-water 1:3 (v/v) ratio (26). Diluent of 187 l ha^{-1} produced a greater canopy reduction than either 37 or 935 l ha^{-1} in honey mesquite, winged elm, and Macartney rose (*Rosa bracteata* J. C. Wendl.) using the ester form of 2,4,5-T at 0.56 and 2.2 kg ha^{-1} on honey mesquite and winged elm and 2.2 kg ha^{-1} of 2,4-D ester on Macertney rose. When 1.1 kg ha^{-1} of MCPA was used on white brush, there were no differences in 37,187 or 935 l ha^{-1} diluent but 187 l ha^{-1} of diluent was superior to other spray volumes on live oak using 2.2 kg ha^{-1} of 2,4,5-T. A diluent volume of 37 l ha^{-1} may have resulted in insufficient coverage for maximum herbicide uptake for most species when ground equipment was used, whereas 935 l ha^{-1} may have resulted in loss of the herbicide from plant surfaces through excessive runoff, except with live oak.

pH Affects

Uptake of 2,4,5-T-1-^{14}C by honey mesquite leaflets immersed in solutions rapidly diminished as pH was increased from 3.5 to 9.5 in the treating solution (11). Leaves treated with droplets at pH 3.5 and kept moist absorbed about 92 percent of available 2,4,5-T-1-^{14}C during the first 3 hours of exposure, with no additional uptake for the next 2 hours. Comparable leaflets treated with droplets that were allowed to evaporate absorbed only 30 percent of available 2,4,5-T-1-^{14}C during the first 3 hours and an additional 10 percent the next 2 hours. Leaflets continued to absorb 2,4,5-T-1-^{14}C for about 14 to 24 hours after treatment with pH 3.5 droplets that were allowed to evaporate, but those kept moist did not absorb 2,4,5-T-1-^{14}C after 3 hours, presumably because of lack of available 2,4,5-T-1-^{14}C. Uptake under dry conditions from pH 7.5 and 9.5 droplets containing 1 M NH_4 Cl was equivalent to uptake from pH 3.5 and 5.5 droplets lacking NH_4 C1. NH_4 C1 had no enhancing effect on uptake at

any pH when leaflets were immersed or droplet-treated and maintained moist. Low concentrations of urea had no enhancing effect on uptake at pH 9.5 by droplet-treated leaflets that were allowed to dry. Urea concentrations above 0.1 M inhibited uptake.

Discs of potato (*Solanum tuberosum* L.) tuber tissue were immersed in buffered (pH 4.0 to 8.0) solutions of picloram ($5x10^{-4}$ M to $5x10^{-3}$ M) for 1 to 36 hours (100). Uptake of picloram during incubation, and leakage after return of the discs to untreated buffer, were determined by gas chromatographic analysis of extracts of the tissue and ambient buffer. Picloram absorption increased with concentration and with time up to 24 hours. Maximum uptake occurred at pH 4.0 and very little picloram was absorbed at pH 7.0 and 8.0. Both absorption and leakage were temperature dependent. The rate and extent of leakage was greatest at the highest concentration. Typically, more than 90 percent of the picloram absorbed from a $5x10^{-3}$ M solution was lost to fresh buffer within 12 hours.

Detached live oak leaves were immersed in aqueous solutions of picloram or 2,4,5-T acid for periods up to 4 hours. (7). Herbicide concentration ranged from 10^{-3} to 10^{-6} M; solutions were adjusted to either pH 4, 6, 7, or 8. More 2,4,5-T was absorbed at pH 4 than pH 6, 7, or 8 at concentration of 10^{-3} M solutions. More picloram was absorbed at pH 4 and 6 than pH 7 or 8. Under laboratory conditions, weak acids penetrate best at low pH values where the molecules are largely in the undissociated form (44,46). In this state, they more readily penetrate the lipoidal phases of the cuticle and leaf cells. However, under field conditions, little benefit of improved control has been shown by adjusting pH of the spray solution.

Mayeux and Johnson (76) found that absorption decreased with increasing pH of the picloram solution in detached pricklypear pads indicating that picloram diffused through the cuticle as the undissociated molecule.

Air Temperature and Relative Humidity

Morton (88) treated honey mesquite seedling leaves with 5 to 100μg of carboxyl-labeled 2,4,5-T and found more 2,4,5-T absorbed at 38 C than at 21 or 29 C after 72 hours. Approximately 50 percent of the 2,4,5-T applied to a single leaf was absorbed. Only slight differences in absorption were found at different humidity levels. Baur et al. (11), however, suggested that humidity effects are of more importance in foliar application than are pH effects since uptake of 2,4,5-T ^{14}C by honey mesquite leaflets under high-humidity surpassed uptake under low-humidity conditions.

Rainfall

Bovey and Diaz-Colon (19) found that oil-soluble formulations (esters) of 2,4,-D, 2,4,5-T, and picloram were less affected by artificial rainfall than water-soluble herbicides such as paraquat and cacodylic acid on guava (*Psidium guajava* L.) and mango (*Mangifera indica* L.). The oil-soluble phenoxy herbicides usually retained their effectiveness even when leaves were washed within 15 minutes after treatment. Field-grown honey mesquite leaves showed complete leaf necrosis even when leaves were washed 20 minutes after treatment with paraquat, indicating rapid absorption (16). Winged elm and live oak showed little injury under the same conditions but both showed about 40 percent leaf necrosis when washed 60 minutes after treatment.

The foliar activity of the amine salts of glyphosate, dicamba, picloram, clopyralid, and triclopyr was decreased on greenhouse-grown huisache when simulated rainfall was applied up to 240 minutes after herbicide treatment (39). The effectiveness of the butoxyethyl ester of triclopyr or 2,4,5-T was not reduced by rainfall washoff within 15 minutes after application. In natural huisache stands, injury from triclopyr ester or amine salts of picloram or clopyralid was not reduced by simulated rainfall at 60 minutes after herbicide treatment. In the greenhouse and field, honey mesquite leaves rapidly absorbed most herbicides and triclopyr, 2,4,5-T, picloram, and clopyralid were highly phytotoxic even when simulated rainfall was applied within 15 minutes after herbicide treatment (39).

Time of Day

No absorption data are available for huisache or Macartney rose relative to time of day or season of application. However data suggested that 1 to 1 ratios of picloram plus 2,4,5-T as the triethylamine salts were more effective when applied to these woody plants in the evening (6:00 p.m.) than morning (6:00 a.m.) or midday (1:30 p.m.) (24). Best control of huisache was in

June while best control of Macartney rose occurred in September and October. Poorest control occurred when internal water stress was highest.

Moisture Stress

Merkle and Davis (80) showed that foliar absorption of 2,4,5-T and picloram in beans (var. Black Valentine) was unaffected by extreme moisture stress. Moisture stress reduced foliar uptake of picloram in honey mesquite but not in winged elm (48). Moisture stress did not affect absorption of 2,4,5-T in honey mesquite or winged elm.

Bovey and Clouser (41) found in preliminary studies that water stress (-1.3 to -2.8 MPa) did not affect absorption and translocation of clopyralid in greenhouse-grown honey mesquite 4 or 24 hours after herbicide treatment. Addition of triclopyr (synergistic to clopyralid) increased clopyralid uptake at low water stress (-1.3 MPa) but at high water stress (-2.8 MPa) triclopyr decreased clopyralid uptake.

Light

Light assists herbicidal penetration by stimulating stomatal opening in most species (1). Measurement of herbicide absorption by honey mesquite as influenced by quality and intensity of light has not been determined. Brady (15), however, found that the absorption of the isooctyl ester of 2,4,5-T increased as light intensity increased up to 2,680 foot candles, but it decreased thereafter in post oak (*Quercus stellata* Wangenh.) and water oak (*Quercus Nigra* L.). Absorption of 2,4,5-T increased as light intensity increased up to 4,000 foot candles in long leaf pine (*Ilex opaca* Ait.). Davis et al. (49) found that uptake of picloram by live oak leaves decreased as light intensity increased.

Scifres et al. (96) found that honey mesquite seedlings which developed under shade were more easily killed by 2,4,5-T sprays than seedlings grown in sunlight. The increased effectiveness under shade may have been caused by limited cuticle development (64) and, thus, greater herbicide uptake. Baur and Swanson (3) found that honey mesquite grown during short days was more susceptible to 2,4,5-T or picloram than that grown during long days. The reason for this difference is not clear but may be related to cuticular development.

Leaf Structure and Development

As indicated earlier, the best time for application of foliar herbicides for honey mesquite control is during a 50- to 90-day period after the first leaves emerge in the spring. By May 20, leaflets of honey mesquite in Brazos County have usually attained full maturity (81). The upper cuticle is usually 5 to 8 microns thick and the lower cuticle is usually 2 microns thick; however, penetration of cuticle by herbicides appears sufficient for herbicidal effect and translocation to other parts of the plant. In most plants, there is a relationship between cuticular development and composition and foliar absorption of herbicides (64). The more mature the leaf, the greater the cuticular development, and that may partially explain the resistance of honey mesquite to herbicide sprays applied late in the growing season, even though limited stomatal penetration can occur when cuticules become very thick (64). Mayeux and Jordan (74) found that amounts of epicuticular wax per unit leaf area on honey mesquite leaves were least in April and May, increased until July, and remained stable thereafter at several locations in Texas. Population means ranged from ca 4 mg dm^{-2} in east-centeral Texas during April and May to a maximum of over 10 mg dm^{-2} on leaves of trees growing in north-centeral Texas in October. Honey mesquite growing in arid-west Texas and semiarid south Texas had no more wax per unit leaf weight or area than those in humid east-central Texas. Mayeux and Wilkerson (77) also determined the chemical composition of epicuticular wax on honey mesquite. Jacoby et al. (65) studied wax on leaves of honey mesquite in northeastern Texas. They found trends similar to Mayeux and Jordan in wax accumulation on honey mesquite leaves but found considerable variation in wax accumulation among individual trees. Jacoby et al. (65) further stated that increasing amounts of epicuticular wax on the leaves of honey mesquite during early summer may contribute to increasing resistance to foliar-applied herbicides.

Wax thickness on honey mesquite may act as a herbicide barrier, but data indicate that most herbicides used are rapidly absorbed and transported by honey mesquite leaves (11, 28, 30,

31, 32, 33, 35, 36, 37, 38, 39, 41, 48, 49, 56, 62, 88, 94, 107)). Bovey et al. (31) found that concentrations of 2,4,5-T, triclopyr and picloram in upper stem pholem and xylem 3 days after treatment to be greater in early May or late April than late May, June, July, August, or September but differences were not always significant. Control with 2,4,5-T, picloram, and triclopyr declined in July, August, and September (87) but is related to anatomical and physiological changes in honey mesquite plants instead of leaf wax accumulation (81). Meyer et al. (87) and Jacoby et al. (66) reported successful late season application with clopyralid on honey mesquite. Data on clopyralid concentrations in honey mesquite in upper stem phloem and xylem 3 days after treatment over a 2-year period showed no differences among dates of sampling (31). Higher than normal rates were used (1.1 kg ha^{-1} versus 0.28 or 0.56 kg ha^{-1}) . Mayeux et al. (68) indicated that poor herbicide uptake by spiny aster top-growth was not adequately explained by cuticle thickness but that chemical characteristics of the epidermal covering may be more responsible for high resistance to herbicide penetration than cuticle thickness. Large quantities of viscous, non-crystilline epicuticular waxes were observed on leaves of three goldenweed (*Isocoma*) species (72). Wax on leaves of field-grown plants of the least herbicide-susceptible species, common goldenweed [*I. coronopifolia* (Gray) Greene.], increased from 71 mg dm^{-2} in March to 286 mg dm^{-2} in October. This was two to four times greater than the amount present on other goldenweed species or Drummond's goldenweed [*I. drummondii* (T. & G.) Greene.] and jimmyweed [*I. Wrightii* (Gray) Rydb.]. Greenhouse-grown plants produced quantities similar to field-grown plants, but maximum production occurred during summer months. Wilkerson and Mayeux (105) determined that the chemical composition of epicuticular wax of *I. coronopifolia* and *I. drummondii* was 85 to 95 percent free fatty acid and alcohols. Alkane (< 5 percent), ester (< 2 percent) and ketone (<3 percent) concentrations were low. The short-chain, free fatty acids and alcohols suggested that they are hydrophilic compared with other plants and helps explain the observed loss of epicuticular waxes in rainfall (71, 75) and variation in responses of these weedy shrubs to herbicide sprays (67, 69, 73). Control of *I. coronopifolia* and *I. drummondii* with broadcast sprays of translocated herbicides strongly depends upon substantial rainfall prior to treatment (71). Removal of leaf waxes increased picloram accumulation in detached leaves of both species by a factor of eight, demonstrating that these deposits effectively reduce herbicide entry (69). Mayeux and Johnson (76) found that removing the epicuticular wax from mature pads (cladophylls) of Lindheimer pricklypear cactus increased picloram absorption by four-to six fold while addition of surfactant had little effect on absorption. Picloram entered detached pads at the areoles more readily than through the surrounding cuticle. New pads absorbed more picloram than old pads. Most of the picloram remained in the waxy surface of old and new pads. About 2 percent of applied picloram was recovered from within the epicuticular wax after 30 days. Little picloram was absorbed by roots. Wilkerson and Mayeux (106) determined that 97 percent of total epicuticular wax of *O. engelmanii* was alkanes and esters on greenhouse-grown cladoyphylls. The most prevalent carbon numbers of alkanes from buds were C_{15} through C_{25} while those of fully expanded cladophylls were C_{29} through C_{35}. Both odd and even numbered ester components were present.

The abaxial (lower) surface of the leaf usually absorbed more herbicide than the adaxial (upper) surface using picloram or 2,4,5-T on 10 species of woody plants (49). Absorption through leaf surfaces varies from abaxial to adaxial on the same species and between species. Meyer and Meola (85) have provided data on leaf and stem surfaces of many Texas woody plants.

Metabolism Degradation and Mode of Action

Morton (90) found that approximately 80 percent of the 2,4,5-T absorbed by leaves of honey mesquite seedlings was metabolized after 24 hours. Metabolism was completely inhibited at 10 C, and a lower rate of metabolism was noted at 38 C than at 21 C and 29 C. Picloram, however, is more resistant to degradation in plants than 2,4,5-T (22).

The effects of picloram on protein synthesis in bean (var. Astro) hypocotyl and hook tissues were studied (8). Picloram (10^{-4} M) was shown to have a stimulatory effect on ^{14}C-1-DL-leucine uptake in hook but not hypocotyl tissues. Maximum leucine incorporation and max-

imum total protein concentration occurred in hook tissues treated with 10^{-4} M picloram. Inhibition of protein synthesis with cycloheximide (CH) and erythromycin (ERY) indicated that endogenous and picloram-stimulated protein synthesis is a function of the 80S cytoplasmic ribosomes rather than 70S chloroplast or mitochondria ribosomes.

Gas chromatographic and radioisotopic analyses were made of cell wall, chloroplast, mitochondria, and the remaining cytoplasm fractions of cowpea (*Vigna sinensis* Endl. var. Southern Blackeye) trifoliates acropetal to primary leaves treated with the growth regulator picloram (9). The majority of picloram was recovered from the remaining cytoplasm. Concentrations in chloroplasts and mitochondria were consistently low.

Pretreatment of potato (*Solanum tuberosum* L., var. Russet) tuber discs in pH 5.5 buffer significantly reduced uptake of picloram (10^{-3} M) (6). Tissue pretreated in buffer at 7 C subsequently absorbed more picloram than tissue pretreated at 25 C. Inclusion of cetyl trimethyl ammonium bromide (CTAB) ($2x10^{-4}$ M) in the treating solution caused a significant increase in picloram uptake in tissues that were not pretreated in buffer. The reduction in uptake caused by buffer pretreatment was effectively reversed when CTAB was included in the treating solution. The results suggest that picloram uptake by potato tissue is related to the availability of the quaternary ammonium binding sites provided by membrane phosphatides.

In nutrient agar, comparative concentrations (10^{-3} to 10^{-5} M) of 2,4,5-T generally inhibited the growth of tissue cultures of soybean (var. Acme) and cottonwood more than either picloram or dicamba (52). Compared to untreated tissue, dicamba or picloram at 10^{-6} M in the nutrient agar resulted in a 200 percent increase in the growth of soybean tissue. At 10^{-5} and 10^{-6} M dicamba also produced an increase in the growth of cottonwood tissue. Greatest absorption of picloram and dicamba by tissue cultures from agar occurred during the first 24 hours after treatment. However, absorption remained nearly static thereafter for 14 days. More dicamba was absorbed by soybean and cottonwood tissue cultures than either picloram or 2,4,5-T. In another study (23), mixing equimolar solutions of 2,4,5-T plus dicamba, 2,4,5-T picloram, or picloram plus dicamba at 10^{-4}, 10^{-6}, and 10^{-8} M did not increase phytotoxicity over that of the most phytotoxic herbicide of the pair.

We studied changes in the concentration of picloram with time in roots, stems, and leaves of 20-day-old seedlings of huisache and honey mesquite (4). Exposing root systems to aqueous solutions of picloram (1.0 ppm on huisache and 10.0 ppm on honey mesquite) for 24 hours killed approximately 60 percent of the treated plants. In honey mesquite, picloram was redistributed and eventually lost over a 5-day period, whereas neither redistribution nor loss occurred in huisache.

Honey mesquite leaves absorbed large amounts of clopyralid as foliar sprays by concentrations of 10 μg or more of the herbicide per gram (fresh wt) of the basal stem phloem by 4 days after treatment. (35). Small quantities of clopyralid (< 1 $\mu g\ g^{-1}$) were detected in basal stem phloem after spray applications of clopyralid to defoliated plants or roots of foliated plants treated by soil application. When applied to foliated plants, the 0.56 kg ha^{-1} of clopyralid killed 60 percent or more of the plants, but none were killed when clopyralid sprays were applied to defoliated plants or when 2.2 kg ha^{-1} of clopyralid was applied to the soil. Water, diesel oil plus water, or water plus surfactant were equally effective as clopyralid carriers as foliar sprays.

Translocation

Once an herbicide is absorbed by leaves and stems, a key factor in killing woody plants is translocation of the phytocide to the stem and roots. The phloem is the principal food-conducting tissue in vascular plants. Compounds like 2,4-D are translocated through the phloem from regions of carbohydrate synthesis (leaves) to sugar importing tissues such as roots, buds, shoot tips, seeds and fruit, and other leaves. The direction of herbicide movement is determined by the patterns of food distribution and utilization within the plant, since translocation of food may also occur from roots to leaves or between other plant parts (44, 45, 46, 47). Ideally, at least for the phenoxy herbicides, it is best to apply foliar sprays when food transport is occurring form the leaves (basipetal) to other plant parts (roots) so as much herbicide as possible is translocated to the base of the stem and roots. In the case of honey mesquite, this occurs under springtime conditions after foliage is mature enough to export sugars and

the plant is rapidly growing radially. If the herbicide is applied at other times during the year, results may be unsatisfactory since assimilate (food) movement may be limited. For successful chemical control of honey mesquite, movement of phytotoxic materials to regenerative tissues (buds) is necessary to eliminate their growth potential. The greatest concentration of buds occurs on the trunk in the first 30 cm below the soil line (53, 57, 58, 81, 95).

Herbicide Type

Fisher and Young (54) reported in 1948 that sodium arsenite, sodium arsenate, sodium chlorate, ammonium sulfamate, sulfamic acid, ammonium thiocyanate, 2,4-D, and 2,4,5-T were the only chemicals out of several hundred tested that were absorbed by the foliage and translocated in sufficient amounts to kill dormant buds on the underground stems of honey mesquite. Increasing chemical concentrations did not improve translocation. In 1949, Young and Fisher (108) reported that the ester of 2,4.5-T was a more effective treatment than several formulations of 2,4,-D or other chemicals.

Rapid transport of 2,4,5-T was determined by plant response after spraying an exposed branch of honey mesquite and observing the effect on leaves of sprayed compared with a shielded or protected plant part. (107). Fisher and Young (88) also used a tip immersion method to test translocation by immersing the tip of a branch into a container of herbicide for periods of 1 to 24 hours and observing translocation by plant response. These methods were very useful in determining the most effective transported herbicides but did not quantitively measure herbicide content in plant tissue.

Early in the 1960s, picloram and dicamba were discovered to be effective herbicides for controlling honey mesquite and other woody plants. Triclopyr and clopyralid were evaluated as substitute herbicides for 2,4,5-T in the late 1970s, 1980s and 1990s (32).

Merkle and Davis (79) recovered 76 percent of the 2,4,5-T and 94 percent of the picloram from bean plants (Black Valentine) 4 hours after application to a primary leaf. Most of the 2,4,5-T and picloram was found in the treated leaf and leafwash but small quantities of picloram was detected throughout the plant including the roots. Probably considerable metabolism of 2,4,5-T occurred since recovery was only 76 percent (88). Data are similar in honey mesquite seedlings to beans in that mesquite absorbed piclorams more readily and extensively than 2,4,5-T (48). After 4 hours, the apex contained both herbicides but only picloram occurred in roots. After 24 hours, the apex and roots contained more picloram than 2,4,5-T. The amounts of picloram and 2,4,5-T absorbed and transported in winged elm were similar.

In the field, Davis et al.(51) found that 2,4,5-T content in honey mesquite stem phloem was higher in stems within 20 cm of the foliage than those near the soil line 48 hours after treatment. Similar levels of 2,4,5-T occurred from application of either 0.56 or 1.12 kg ha^{-1} whereas, three times as much picloram occurred in plants treated with 1.12 kg ha^{-1} than with 0.56 kg ha^{-1}. Herbicide concentration was highest in June and lowest in August.

Meyer et al. (82) indicated the time required by herbicides to be retained on the plant after spraying to give maximum canopy reduction or mortality varied among greenhouse-grown honey mesquite, huisache, and whitebrush [*Aloysia gratissima* (Gillies & Hook.) Troncoso] and field-grown honey mesquite, huisache, whitebrush, live oak, Arizona ash (*Fraxinus velutina* Torr.), and winged elm. In most species, however, herbicide absorption and transport were complete within a 4-day period or less as compared to undefoliated treated plants.

Bovey and Mayuex (28) studied the effectiveness and transport of 2,4,5-T, picloram, triclopyr, and clopyralid in greenhouse-grown honey mesquite. Higher concentrations of clopyralid than 2,4,5-T, triclopyr, or picloram usually were found in honey mesquite stems and roots 3, 10, and 30 days after application to soil, foliage, or both. This may be one reason why clopyralid is highly effective in controlling honey mesquite. In other studies, concentrations of clopyralid and picloram in upper-stem phloem were not different 4 hours after treatment, but clopyralid concentrations were significantly higher than picloram at 1, 3, and 8 days after treatment in greenhouse-grown honey mesquite (36).

In the field and greenhouse, Bovey et al. (28, 31) found comparisons of triclopyr, 2,4,5-T, picloram, and clopyralid similar to studies by Davis et al.(51) who compared picloram and

2,4,5-T on honey mesquite. More clopyralid than 2,4,5-T, triclopyr, or picloram was usually detected in upper and basal stem phloem and xylem. Concentrations of 2,4,5-T and triclopyr in stem tissue were usually <2 $\mu g\ g^{-1}$ fresh wt, regardless of date of application. Concentrations of picloram or clopyralid were as high as 11 and 22 $\mu g\ g^{-1}$ fresh wt, respectively, in upper stem phloem at some dates of application. Higher concentrations of all herbicides were detected in upper stem phloem than in upper stem xylem or basal stem phloem or xylem. More herbicide tended to be detected in stems when herbicides were applied early (May and June) than late (August and September) in the season. Concentrations of triclopyr and picloram diminished about 25 percent from 3 to 30 days after treatment, whereas, concentrations of 2,4,5-T and clopyralid diminished about 50 percent for the same time period.

Bovey et at. (17) found that soil applications of picloram were more effective on greenhouse-grown huisache than foliar treatments. However, soil and foliar applications at 0.56 kg ha^{-1} were lethal on foliated plants whereas hand defoliated plants showed considerable regrowth. Plants treated with 0.28 kg ha^{-1} required 24 hours before leaf removal for maximum herbicide effectiveness. Concentration of picloram in roots from soil and foliar application was similar. Absorption and movement studies showed that 24 hours were required to move lethal amounts of picloram into stem and root tissues of huisache after foliar treatment.

Further research by Bovey et al. (27) indicated that more picloram than triclopyr was found in greenhouse-grown huisache up to 30 days after treatment as soil, foliar, or soil plus foliar treatments. Picloram also showed greater herbicidal activity.

Mayeux (68) found spiny aster absorbed little herbicide relative to that in annual sunflower. Spiny aster absorbed and transported more 2,4-D than picloram when applied as the potassium salts of both herbicides by 4 and 6 hours after treatment. In general, 2,4-D behaved similarly when applied to leafless spiny aster in June and to foliated spiny aster in March. Concentration of 2,4-D in terminal stems of regrowth 74 days after shredding rose rapidly to almost 19 $\mu g\ g^{-1}$ fresh wt at 24 hours after application and gradually fell to about 5 $\mu g\ g^{-1}$ after 120 hours. Maximum 2,4-D concentration in terminal stems of undisturbed spiny aster was less than 14 $\mu g\ g^{-1}$. Picloram concentrations in terminal stems were highly variable. There were no differences in herbicide concentrations in shredded and nonshredded terminal stems. No 2,4-D or picloram was detected in rhizomes.

Drummond's goldenweed leaves absorbed about 50 percent of available 2,4-D (diethylamine) and 25 percent of available picloram (potassium salt) within 5 days after spraying in the field during July or November (70). Herbicide accumulation in Drummond's goldenweed taproots after spray applications was generally slow, regardless of season, but translocation to taproots was substantially greater after application in November than after treatment in March or July. Accumulation of picloram in taproots was faster and more extensive than accumulation of 2,4-D. However, based on mortality at 6 months after treatment, both herbicides were translocated in quantities adequate for control. The greater effectiveness of picloram, despite its low foliar uptake, than 2,4-D is attributed to its greater mobility and root uptake in Drummond's goldenweed after broadcast sprays.

More picloram was translocated basipetally from treated new pricklypear pads to untreated old pads than in the opposite direction, but concentrations in untreated pads were low (<1 $\mu g\ g^{-1}$) (76). Little picloram was absorbed by roots, compared with pads, and little was translocated into or out of roots. These results conflict with the view that the effectiveness of picloram for pricklypear control is attributable to extensive root uptake and acropetal transport. However, observations of plants 6 months after treatment indicated that soil applications were more effective than sprays in the glasshouse.

Herbicide Formulation

Although Morton et al. (89) found larger amounts of 2,4,5-T in honey mesquite leaves treated with the butoxyethyl ester than the ammonium salt, concentrations of 2,4,5-T in the stem were equal. Hull (62) reported in velvet mesquite that when carried in a nontoxic oil emulsion, the free acid, the triethylamine, and the sodium salts of 2,4,5-T all demonstrated a greater tendency to be translocated to more distant portions of the plant than did ester formulations. Tschirley and Hull (101),

however, found the ester of 2,4,5-T consistently more effective than the amine formulation on velvet mesquite under field conditions. Research data of Fisher et al. (57) on honey mesquite agree with that of others (101) in that the low volatile esters and suspended acids were more consistent in killing mesquite than either the high volatile esters or the amine formulations. The reasons for the superior performance of the ester of 2,4,5-T over the amine formulation has not been clearly established, but the ester formulation probably penetrates the wax and cuticle on the leaf more readily than the amine. However, Beck et al. (12,13) showed little difference in effectiveness between the ester and amine formulations of 2,4,5-T on honey mesquite. Differences in formulation may have been masked by high rate of application or by the fact that sprays were applied to the base of the plants.

Bovey and Mayuex (28) found no differences between the ethylene glycol butyl ether esters or triethylamine salt of triclopyr in greenhouse-grown honey mesquite stems and roots 3,10, and 30 days after aqueous applications to the soil, foliage, or soil plus foliage.

In other detailed studies, triclopyr was rapidly transported from the treated leaf to other plant parts. Triclopyr concentrations recovered 4 hour after treatment in the upper canopy, lower canopy, and roots averaged 0.12, 0.19, and 0.09 μg, respectively (30). Concentrations of triclopyr recovered after 24 hours were not significantly different than after 4 hours in the canopy. No ester from ester application was recovered in the canopy, other than that in the treated leaf. Uptake and transport of triclopyr applied as either the ester or the amine 4 and 24 hours after treatment were similar. Triclopyr recovered from stems of honey mesquite in the field ranged from 0.16 to 0.72 $\mu g\ g^{-1}$ in phloem and from 0.04 to 0.20 $\mu g\ g^{-1}$ in xylem from a broadcast spray application of the butoxyethanol ester at 1.12 kg/ha^{-1}. Concentrations of triclopyr were usually not significantly different in either the upper or lower stems whether sampled 3 or 30 days after treatment.

Foliar sprays of the monoethanolamine salt, potassium salt, free acid, and 1-decyl ester of clopyralid were more effective in killing greenhouse-grown honey mesquite than the 2-ethylhexyl ester at rates of 0.28 kg ha^{-1} or less (37). More clopyralid was transported to the lower canopy from application of the monoethanolamine salt and potassium salt than the 2-ethylhexyl ester of clopyralid at 4 hours or 1, 3, or 8 days after treatment. Application of the monoethanolamine salt and the 2-ethylhexyl ester to leaves with a pipet indicated that about twice as much clopyralid was absorbed within 15 min from the ester form (26 percent) than from the amine form (12 percent) of the total recovered. However, after 24 hours, absorption of the ester was less than the amine. More than twice as much clopyralid was transported from the treated leaf after application of amine than the ester. Only the acid form of clopyralid was transported away from the site of application of either ester or amine.

Foliar sprays of the monoethanolamine salt, oleylamine salt, and 1-decyl ester of clopyralid were about equally effective in killing greenhouse-grown honey mesquite (38). Treated leaves absorbed more clopyralid within 15 min after pipet application of the oleylamine salt compared with the other formulations. After 24 hours, treated leaves had absorbed and transported more clopyralid into the plant from the salt formulations than the 1-decyl ester. There were no consistent differences among clopyralid formulations in transport of clopyralid from foliar sprays at 4 hours or 1, 3, or 8 days after treatment. Only the acid form of clopyralid was transported from the site of application of either ester or the amine formulation.

Herbicide Mixtures

The combination of picloram and 2,4,5-T (18, 92) was particularly useful in honey mesquite control. Davis et al. (50) in 1968 found that transport of picloram to the lower stem in greenhouse-grown honey mesquite was increased in the presence of 2,4,5-T whereas the uptake and transport of 2,4,5-T was decreased in the presence of picloram. Increasing ratios of 2,4,5-T to picloram in mixtures up to 16 to 1 continued to increase uptake and transport of picloram; the reverse effect occurred for 2,4,5-T when 2,4,5-T to picloram ratios were decreased. More total herbicide was transported when the 2,4,5-T and picloram combination was used than either herbicide used alone at equal rates. This may help to explain the greater effectiveness of the herbicide combination in controlling honey mesquite. When paraquat was combined with picloram on honey mesquite, huisache, and bean, transport of picloram to the lower stem

was reduced because of damage of the transport system by paraquat.

In field studies, Davis et al. (51) found that highest concentrations of 2,4,5-T, picloram, or combinations of 2,4,5-T and picloram in phloem were associated with dates of best control of honey mesquite established by numerous investigations. Adding 2,4,5-T to picloram caused an increase in the amounts of picloram in the phloem in four of five dates of application (51). These data agree with the laboratory and greenhouse investigations previously described (50). Therefore, the combination of picloram and 2,4,5-T was generally more effective than either herbicide applied alone.

Recovery of 2,4,5-T as the acid and ester was significantly greater in live oak tissues treated with mixtures of the 2-ethylhexyl ester of 2,4,5-T (2.2 kg ha^{-1}) plus the potassium salt or isooctyl ester of picloram (0.56, 1.1, and 2.2 kg ha-1) than in tissues treated with 2,4,5-T ester alone (5). Recovery of 2,4,5-T as the ester was noted in the middle and lower-stem tissues. Between 90 and 99 percent of the herbicide recovered 1 month after treatment was gone 6 months after treatment. Evaluation of brush reduction 2 years after treatment indicated that mixtures of picloram salt and 2,4,5-T resulted in greater reduction of brush than mixtures of picloram ester and 2,4,5-T or 2,4,5-T alone.

Bovey et al. (36) found that the addition of picloram or triclopyr to clopyralid at equal rates (0.28 + 0.28 kg ha^{-1}) increased clopyralid concentrations in field-grown honey mesquite by 1 day after treatment compared to clopyralid applied alone.

Carriers and Adjuvants

A large number of diluents and adjuvants for herbicides have been evaluated for control of woody plants with some success (26, 32, 57, 62) as discussed in the Carriers and Adjuvants section under Foliar Absorption.

An April application of 1.12 kg ha^{-1} or picloram plus 5.0 percent X-77 plus 10.0 or 25.0 percent of DMSO produced more effective canopy reduction of yaupon 1 year after treatment than did other herbicide treatments or dates of treatment (10). Increased canopy reduction by retreatment the second year suggests that X-77 rather than DMSO was the effective component in the spray mixtures.

Scifres et al. (94) compared water, diesel oil, diesel oil and water emulsion (1:4), paraffin oil, and paraffin oil and water emulsion (1:4) for carriers of 0.56 kg ha^{-1} of the butyl ether ester of 2,4,5-T in greenhouse-grown honey mesquite. No differences related to carrier occurred in the amount of 2,4,5-T translocated to the stem and roots, although greater amounts of herbicides were absorbed by leaves treated with diesel or paraffin oil carriers.

Concentration of clopyralid in basal stem phloem of field-grown honey mesquite sampled 4 and 30 days after spraying 0.56 kg ha^{-1} to the foliage showed no differences in water, diesel oil plus water (1:4 v/v), and water plus 0.5 percent surfactant (v/v) diluents (35). Surfactant I (trimethylnonylpolyethoxyethanol) or surfactant II (4-Isoprophenyl-1-methyl-cyclohexane) at 0.5 percent by volume of the spray solution enhanced clopyralid absorption and transport to the upper stem phloem in field-grown honey mesquite by 1 day after spraying 0.28 hg ha^{-1} clopyralid (36). Enhanced absorption and transport of clopyralid may be partially explained by the enhanced spray retention of clopyralid on the leaves with use of a surfactant (33, 36, 40).

Organosilicone surfactants, Silgard 309 or Silwet L-77, added to the spray solutions at 0.1, 0.25, or 0.5 percent by volume did not increase spray deposition, absorption, translocation, or phytotoxicity of clopyralid in greenhouse-grown honey mesquite (42).

Spray Characteristics

The addition of surfactant WK at 0.5 percent (v/v) caused increased uptake of clopyralid by the upper canopy of greenhouse grown honey mesquite (33). Enhanced uptake after 24 hours was probably a result of a twofold increase in deposit of clopyralid on the plant (33, 40). Greater deposit of clopyralid on plant surfaces after addition of surfactant was associated with reduced liquid surface tension and greater percentage of spray volume in small droplets (< 204 μm diam.). The addition of surfactant WK at 0.5 percent (v/v) of the spray solution caused a twofold increase in deposition of the monoethanolamine salt of clopyralid but not the oleylamine salt (40). There were no differences in spray deposit between spray droplet size spectrums of 160 or 330 μm Dv.5 or spray solution application of 47 or 187 l ha^{-1}.

An air-assist spray nozzle at 9.4 l ha^{-1} by volume resulted in greater initial clopyralid deposit and detection in the upper canopy of greenhouse-grown honey mesquite than application by conventional hydraulic nozzle at 9.4 or 187 l ha^{-1} (42). Air-assist application did not increase phytotoxicity compared with hydraulic nozzles. In the field, honey mesquite mortality and canopy reduction 16 months after aerial application of clopyralid were significantly less in the 624 μm droplets treatment in two of four experiments, when compared with plots treated with smaller droplet sizes (325 and 475 μm Dv.5) (104). Mortality increased with larger spray volumes (19, 37, and 75 l ha^{-1}) particularly with the 625 μm droplet size. Mortality data show that larger droplets sizes require larger spray volumes for greatest efficacy.

pH Affects

See pH Affects under Foliar Absorption.

Temperature and Relative Humidity

Translocation of 2,4,5-T in honey mesquite seedlings was primarily basipetal (downward) from the point of application at 21 C, both acropetal (upward) and basipetal at 29 C, and only a short distance acropetal at 38 C (88). The quantities of 2,4,5-T translocated into untreated tissues at 38 C were less than at 21 C and 29 C. The highest concentrations of 2,4,5-T were found in tissues with highest soluble sugar concentrations. From 3 to 27 percent of the 2,4,5-T absorbed by honey mesquite leaves was subsequently detected in untreated stem, leaf, and root tissues. Total amounts of C^{14} (carboxyl-labeled 2,4,5-T) detected in the untreated tissues of the seedlings tended to increase, particularly in the roots and lower stems, with increasing humidity.

Radosevich and Bayer (90) found that 2,4,5-T, triclopyr, and picloram transport was greater in periods of warm temperatures (29 C day and 13 C night) and long days (16-hour photoperiod) than at cool temperatures (13 C and 2 C day and night) and a 12-hour photoperiod in five plant species as revealed by autoradiographs. They found little metabolism of any herbicide, and each herbicide moved readily in the symplast (phloem); however, root application revealed limited apoplastic (xylem stream) mobility.

Rainfall

See Rainfall under Foliar Absorption.

Time of Day

See Time of Day under Foliar Absorption.

Light

Light intensity affected translocation of 2,4,5-T to the roots of woody plants (15). There was a negative linear relationship between light intensity and 2,4,5-T content of post oak roots. In water oak roots, however, herbicide levels increased as light intensity increased. In longleaf pine and American holly, translocation was not significantly influenced by light intensity. Herbicide translocation in honey mesquite as influenced by light has not been measured.

Moisture Stress

Moderate moisture stress in beans did not have a significant effect on the translocation of picloram but did have on the translocation of 2,4,5-T (80). Advanced stress significantly reduced the translocation of both herbicides. However, translocation of 2,4,5-T was apparently more sensitive to changes in moisture stress than was translocation of picloram. Picloram was more mobile than 2,4,5-T at all moisture stress levels studied. After 4 hours, as much picloram was translocated to the apex and central stem of bean plants from a 24 μg application as there was 2,4,5-T at 8 hours after a 50 μg application. This agrees with studies on honey mesquite in which both herbicides were detected in the apex only 4 hours after treatment, but only picloram occurred in the roots (48). After 24 hours, the apex and roots contained more picloram than 2,4,5-T. The phloem-cortex accumulated greater quantities of picloram than the xylem-pith, indicating major transport via the symplast. After 90 hours, herbicide concentrations in most tissues were unchanged or higher than after 24 hours. These data support observations by Meyer et al. (82) which indicated a period of 3 to 4 days was required for honey mesquite to absorb and translocate herbicide for maximum killing of stems. Moisture stress sufficient to slow growth markedly reduced transport of picloram and 2,4,5-T into untreated tissues.

Bovey *et al.* (24) found that 1 to 1 combination of the triethylamine salts of picloram and 2,4,5-T was more effective on huisache and

Macartney rose when applied in the evening than in the morning or at midday in field studies. Internal water stress of the plants was less at night after the 6:00 p.m. treatment than after the 6:00 a.m. or 1:30 p.m. treatment, allowing more favorable environment for absorption and translocaion of the herbicide.

Bovey and Clouser (41) found in preliminary studies that water stress of -1.3 to -2.8 MPa did not affect absorption and translocation of clopyralid in greenhouse-grown honey mesquite 4 or 24 hours after treatment. Addition of triclopyr (synergistic) to clopyralid increased clopyralid uptake at low water stress (-1.3 MPa) but decreased clopyralid uptake at high water stress (-2.8 MPa).

Other Factors

Meyer et al. (83) sprayed honey mesquite in the field with three herbicides at 14 different dates during 1969 and 1970. Most effective control of honey mesquite occurred from treatments applied between April 30 and July 6. Picloram and a picloram and 2,4,5-T (1:1) mixture were the most effective herbicides. Plant characteristics most closely associated with control included widest translocating phloem thickness, most rapid rate of new xylem ring radial growth, and lowest predawn leaf moisture stress. Environmental variables most clearly associated with honey mesquite control were lower maximum air temperatures of 25 C to 36 C 1 week before treatment, maximum soil temperature of 17 C to 26 C at a depth of 91 cm 1 week before treatment, and decreasing percent soil moisture from 25 to 18 percent at a depth of 61 to 91 cm 1 week before treatment. In subsequent studies (84) of responses to spraying on 36 dates from March to October during a 4-year period, percentage of honey mesquite canopy reduction was directly correlated with total phloem thickness, rate of new xylem ring radial growth, and rate of upward methylene dye movement in the xylem and was inversely correlated with minimum leaf moisture stress. Rate of new xylem ring radial growth and thickness of translocating phloem appeared most often in the equations.

Root Penetration and Translocation

Laboratory and Greenhouse Studies

In the greenhouse, huisache and honey mesquite can be killed by soil applied herbicides and show as much or more picloram, triclopyr or clopyralid content in root tissue up to 30 days after treatment as from foliar sprays (17, 27, 28). However, in the field, huisache and especially honey mesquite are difficult to kill with soil-applied herbicides in heavy clay soils (25, 86)

Baur and Bovey (4) studied changes in the concentration of picloram in roots, stems, and leaves of 20-day-old huisache and honey mesquite plants exposed for different lengths of time. Exposing roots to aqueous solutions of picloram for 24 hours killed about 60 percent of the treated plants. It took 10 times more herbicide to give the same response in honey mesquite (10 ppm) as huisache (1 ppm). In honey mesquite, picloram was redistributed and eventually lost from the plant into the rooting solution over a 5-day period, whereas huisache, a more susceptible plant, showed no redistribution or loss of picloram.

Mayeux and Johnson (76) found in Lindheimer pricklypear that picloram concentrations within pads treated in the glasshouse were greater when the herbicide was applied to new pads (4.6 $\mu g\ g^{-1}$) after 30 days. More picloram was translocated basipetally from treated new pads to untreated old pads than in the opposite direction, but concentrations in untreated pads were low ($< 1\ \mu g\ g^{-1}$). Little picloram was absorbed by roots compared with pads, and little was translocated into or out of roots. These results conflict with the view that the effectiveness of picloram for pricklypear control is attributable to extensive root uptake and acropetal transport. However, observations of plants 6 months after treatment indicated that soil applications were more effective than foliar sprays in the glasshouse.

Field Studies

As indicated earlier, control of honey mesquite by soil-applied herbicides has not been highly effective in the field. However, triclopyr, picloram, and clopyralid are highly effective when applied to soil in pots supporting honey mesquite under greenhouse conditions. Possibly the extensive root system of honey mesquite and impermeable heavy clay soils in some areas may partially preclude effective control under field conditions.

Herbicides such as picloram, dicamba, karbutilate, bromacil, tebuthiuron, and prometon (21, 86, 95, 98) when applied as soil treatments for honey mesquite control, have generally been ineffective at economical rates. However, honey mesquite was more effectively controlled in the field when liquid formulations of karbutilate and tebuthiuron were applied subsurface rather than on the soil surface (86).

Leaves absorbed large amounts of clopyralid as foliar sprays on honey mesquite as indicated by concentrations of 10 $\mu g\ g^{-1}$ fresh wt or more in basal stem phloem by 4 days after treatment (35). Small quantities of clopyralid ($< 1\ \mu g\ g^{-1}$) were detected in basal stem phloem after spray applications of clopyralid to defoliated plants or roots treated by soil application. When applied to foliated plants, the 0.56 kg ha^{-1} of clopyralid killed 60 percent or more plants, but none were killed when clopyralid sprays were applied to defoliated plants or when 2.2 kg ha^{-1} of clopyralid was applied to the soil.

Summary

Research work was initiated using translocated hormone-like herbicides for honey mesquite control in the 1940s. Factors affecting the control of honey mesquite using 2,4,5-T were well defined by the mid-1950s. Evaluating the absorption and translocation of an herbicide in early research was estimated by observing plant response of leaf discoloration, defoliation, abnormal growth, reduced growth, stem discoloration, plant mortality, and eventually, possible regrowth. Although observing and recording plant responses to herbicides is essential for evaluating herbicide activity and effectiveness, it does little to quantify absorption and translocation. Development of radiolabled herbicides and monitoring by gas chromatography (GC) methods have helped quantify herbicide uptake and transport. Research in the 1960s on honey mesquite showed that radioisotopic and GC methods gave comparable results when extraction, cleanup, and analytical procedures were identical. Most data reported herewith used GC methods.

Work reported in the 1940s and 1950s indicated that 2,4,5-T was more readily absorbed and transported in honey mesquite than most other chemicals including 2,4-D. In the 1960s picloram was found to enter faster and accumulate at higher concentrations than 2,4,5-T in several woody species including honey mesquite. By 1980 clopyralid was found to be absorbed and transported in higher concentrations in honey mesquite than 2,4,5-T, triclopyr, or picloram and was also more effective.

In greenhouse-grown honey mesquite, herbicides were detectable in the lower stem within 4 hours after foliar treatment and peak concentrations usually occurred 24 to 48 hours after treatment, suggesting rapid absorption and transport. Similar absorption and transport patterns were found in field-grown honey mesquite.

Not all woody species respond the same way as honey mesquite. Spiny aster absorbed less 2,4-D and picloram than sunflower, and picloram concentration was usually less than 2,4-D in spiny aster leaves. Although peak concentrations of herbicide occurred 24 to 48 hours after treatment in spiny aster leaves, foliar absorption is probably a limiting factor in its poor response to herbicides.

Laboratory and field data suggest that the ester form of 2,4,5-T and triclopyr are more effective on honey mesquite than amine formulations, but the amine forms of clopyralid and picloram are more effective than the ester form. It is sometimes difficult to show differences in uptake and transport between herbicide forms. The 2,4,5-T and picloram (1:1) mixture was synergistic on some woody plants. In honey mesquite, uptake and transport of picloram is increased in the presence of 2,4,5-T in both greenhouse and field-grown plants. Synergistic responses have also been shown with clopyralid and triclopyr and clopyralid and picloram mixtures. Uptake and transport of clopyralid in honey mesquite may be increased when mixed with equal ratios of triclopyr or picloram compared with clopyralid applied alone.

Recovery of 2,4,5-T in live oak was significantly greater in mixture with picloram than in tissues treated with 2,4,5-T alone. Live oak control was best 2 years after treatment where mixtures were used compared with either 2,4,5-T or picloram applied alone.

The effects of herbicide type, formulation, and mixtures are discussed. The influence of foliar spray characteristics including diluents, adjuvants, pH, spray droplet size, and spray volume are indicated for absorption and translocation in woody plants as well as leaf structure and development. Environmental factors such as air temperature, relative humidity, rainfall, light and moisture stress are also reviewed.

Herbicides Discussed

Common Name	Chemical Name
Bromacil	5-bromo-6-methyl-3-(1-methylpropyl)-2,4(1*H*, 3*H*)pyrimidinedione
Cacodylic acid	dimethyl arsinic acid
Clopyralid	3,6-dichloro-2-pyridinecarboxylic acid
Dicamba	3,6-dichloro-2-methoxybenzoic acid
2,4-D	(2,4-dichlorophenoxy)acetic acid
Glyphosate	*N*-(phosphonomethyl) glycine
Karbutilate	*tert*-butylcarbamic acid ester with 3-(*m*-hydroxyphenyl)-1, 1- dimethylurea (*m*-(3,3-dimethylureido) phenyl *tert*-butylcarbamate)
MCPA	(4-chloro-2-methylphenoxy)acetic acid
Paraquat	1,1′-dimethyl-4,4′-bipyridinium ion
Picloram	4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid
Prometon	6-methoxy-*N,N′*-bis(1-methylethyl)-1,3,5-triazine-2,4-diamine
Tebuthiuron	*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N′*-dimethylurea
2,4,5-T	(2,4,5-trichlorophenoxy) acetic acid
Triclopyr	[(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid

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